Inflorescence and Flower Development in *Orchidantha chinensis* T. L. Wu (Lowiaceae; Zingiberales): Similarities to Inflorescence Structure in the Strelitziaceae

By: Bruce K. Kirchoff, Huanfang Liu, and Jing-Ping Liao

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Abstract:

Premise of research. The monotypic Lowiaceae remains the least-known family in the plant order Zingiberales, yet it may hold an important key to unraveling the phylogenetic placement of the families Musaceae, Heliconiaceae, Strelitziaceae, and Lowiaceae. After nine phylogenetic studies, the (Lowiaceae, Strelitziaceae) clade is the only stable clade that has emerged in this half of the order. This study was undertaken to verify the unusual inflorescence and flower structure in *Orchidantha* and to search for new characters that might be used in future phylogenetic analyses. We describe both inflorescence and flower development in a previously unstudied species; confirm inflorescence morphology in the genus; and compare the structure of the inflorescence in the Lowiaceae with that of the Strelitziaceae, its potential sister group. *Methodology*. Standard collection and SEM procedures were used to collect and prepare the material for study. *Pivotal results*. The inflorescence of *Orchidantha* is borne at the end of a vegetative shoot and is composed of two lateral branches that each bear four bracts and a single flower before aborting. The fourth bract and its associated flower form the highly reduced flower cluster (florescence) that characterizes this genus. In technical terms, *Orchidantha* has a polytelic synflorescence that lacks a main florescence (it has a truncated polytelic synflorescence) and bears solitary flowers in coflorescences on determinate enriching branches. The enriching branches produce a fixed number of bracts before aborting (i.e., they are special paracladia). Many of these features are shared with the Strelitziaceae. *Conclusions*. Similarities between the Lowiaceae and Strelitziaceae include inflorescence structure; the presence of a long prolongation of the ovary; and a delay in the formation of the third sepal during flower development, a character that is also shared with the Musaceae. Inflorescence and flower structure is now well established in this small but important family.

Keywords: phylogeny | synflorescence | labellum | enriching branch | paracladia | Orchidantha

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INFLORESCENCE AND FLOWER DEVELOPMENT IN *ORCHIDANTHA CHINENSIS* T. L. WU (LOWIACEAE; ZINGIBERALES): SIMILARITIES TO INFLORESCENCE STRUCTURE IN THE STRELITZIACEAE

Bruce K. Kirchoff,[1,*] Huanfang Liu,† and Jing-Ping Liao†

*Department of Biology, PO Box 26174, University of North Carolina at Greensboro, Greensboro, North Carolina 27402-6174, USA; and †Key Laboratory of Plant Resources Conservation and Sustainable Utilization, Guangdong Provincial Key Laboratory of Digital Botanical Garden, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

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Conclusions. Similarities between the Lowiaceae and Strelitziaceae include inflorescence structure; the presence of a long prolongation of the ovary; and a delay in the formation of the third sepal during flower development, a character that is also shared with the Musaceae. Inflorescence and flower structure is now well established in this small but important family.

Keywords: phylogeny, synflorescence, labellum, enriching branch, paracladia, *Orchidantha*.

Introduction

The Lowiaceae, consisting of the single genus *Orchidantha*, is a small family of approximately 17 species in the plant order Zingiberales, the order that contains the bananas (*Musa*, Musaceae) and the culinary gingers (*Zingiber*, Zingiberaceae). Despite a number of descriptions of new species and two pollination studies, the Lowiaceae remain one of the most poorly studied families in the plant order (Nagamasu and Sakai 1999; Sakai and Inoue 1999; Pedersen 2001; Jenjittikul and Larsen 2002; Dăng Trân and Leong-Škorničková 2010; Leong-Škorničková 2014; Leong-Škorničková et al. 2014; Zou et al. 2014, 2017; Poulsen and Leong-Škorničková 2017; Vislobokov et al. 2017; Syauqina et al. 2019). The vegetative body of *Orchidantha* is rhizomatous (plant ontology [PO]:0004542), with new shoots (PO:0004701) arising from axillary buds (PO:0004709). Despite this relative simplicity, the inflorescence of *O. maxillarioides*, the single species that has been studied in detail, is remarkably complex (Kunze 1986; Kirchoff and Kunze 1995). When the vegetative apex transitions to flowering, it produces two bracts (PO:0009055) and two lateral branches, each in the axil of one of the bracts. The main shoot apex (shoot axis apex, PO:0000037) then aborts without producing any additional organs. Each lateral branch produces a prophyll, two bracts that subtend higher-order branches, a bract that subtends a single flower, and one or two abortive bracts. The apex of the lateral branch then aborts. This pattern of lateral branching, the production of a single flower, and the abortion of the apex repeats on all of the lateral branches. Only the Marantaceae has a more complex inflorescence in the order. Two of the goals of this

[1] Author for correspondence; email: kirchoff@uncg.edu.

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article are to verify this inflorescence structure in an additional species and to compare this description with the taxonomic descriptions that have been published since Kirchoff and Kunze (1995).

Like inflorescence structure, flower development has been studied in only one species of *Orchidantha*, and that study was somewhat incomplete because of the lack of material (Kirchoff and Kunze 1995). The early stages of gynoecium initiation are particularly lacking. The current study will correct this deficiency.

The placement of the Lowiaceae as the sister group of the Strelitziaceae in all but two (Kress 1990; Johansen 2005) of the nine phylogenetic analyses of the order (Kress 1990, 1995; Kress et al. 2001; Specht et al. 2001; Johansen 2005; Kress and Specht 2005; Givnish et al. 2006; Specht and Stevenson 2006; Sass et al. 2016) suggests that there could be undiscovered morphological characters (synapomorphies) that unite the two families. Our final goal is to use the new information about inflorescence and flower development to search for these potential synapomorphies.

Material and Methods

Living material of *Orchidantha chinensis* T. L. Wu, including material for developmental study, was collected from three locations in China: Hewei Mountain, Yangchun, Guangdong Province (阳春河尾山; no voucher); Bai Chong Preserve, Yangchun, Guangdong Province (阳春百涌保护区; voucher: Liu 95006, deposited at SCBG and DUKE); and South China Botanical Garden, Guangzhou (华南植物园; voucher: Chen 72370, deposited at SCBG). The plants were dissected and photographed in the field and preserved in formalin acetic alcohol (Berlyn and Miksche 1976) for later study at the University of North Carolina at Greensboro or overnight in 2.5% glutaraldehyde and 2% paraformaldehyde (Berlyn and Miksche 1976) for study at the South China Botanical Garden.

SEM procedures at the South China Botanical Garden (figs. 7B, 7C, 9F). Bracts and larger floral organs were removed under a dissecting microscope before fixation. Following fixation, all floral buds were washed in phosphate buffer in H_2O three times for 2 h and dehydrated in a graded EtOH series (30%, 50%, 70%, 80%, 90%, 100%, 100%, 100% EtOH). The materials were then freeze-dried in a JFD-320 Freeze Dryer (JEOL, Tokyo), mounted on stubs, gold coated in a JFC-1600 Gold Coater (JEOL), and observed at 10 kV under a JSM-6360LV SEM (JEOL). Charging effects were removed with the shadows/highlights image adjustment used as a smart filter in Adobe Photoshop (Adobe Systems, San Jose, CA).

SEM procedures at University of North Carolina at Greensboro (figs. 6A–6H, 7A, 7D–7H, 8A–8H, 9A–9E). Before observation, the specimens were washed in 50% EtOH, dehydrated with 2,2-dimethoxypropane (Postek and Tucker 1976), stained in fast green (Johansen 1940; Berlyn and Miksche 1976), then transferred to 100% EtOH for dissection. Apexes for dissection were supported in Permatex Black Silicone (Loctite, Rock Hill, CT) that had been immersed in 100% EtOH before it had completely hardened. Immersion in 100% EtOH keeps the silicon pliable while allowing it to retain sufficient resiliency to support the apexes. After dissection, the apexes were stored in 100% EtOH for one to many weeks, transferred to biopsy bags, and critical-point dried in a Pelco critical point dryer (Ted Pella, Redding, CA). Inflorescence and floral apexes were mounted on SEM stubs using carbon- or silver-based adhesive. When necessary, the apexes were further dissected under a binocular dissecting microscope so that bracts and flower parts could be removed. The apexes were coated with gold/palladium using a Pelco 91000 sputter-coater (Ted Pella) and were observed with a Leica Stereoscan 430 SEM. Digital images were captured and saved as TIFF files at a resolution of 1024 × 768 pixels and were arranged into plates using Adobe Photoshop (Adobe Systems). All original photographs and SEMs are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.jdfn2z37t; Kirchoff et al. 2020).

Terminology

Wherever possible, the terms used in this article have been cross-referenced with the PO database through the Planteome server (Cooper et al. 2012, 2017). Unfortunately, many of the terms useful in describing inflorescence structure are not part of the PO database. PO terms are cross-referenced on their first use.

Wherever possible, we have used full words or short phrases to label the figures. Abbreviations have been used only when there was no space for the full label. The abbreviations we use are similar to those in other papers on flower (PO:0009046) development in the Zingiberales (Kirchoff and Kunze 1995; Kirchoff 1997, 1998, 2000, 2003, 2017).

Inflorescence Terminology

The terminology introduced by Troll (1964), as modified by Kunze (1986), is used in this study. This terminology has proved remarkably useful in understanding inflorescence (PO:0009049) structure in the Zingiberales (Kunze 1983, 1984, 1985, 1986; Kirchoff and Kunze 1995), though Troll's (1964) typological system has been widely criticized (Briggs and Johnson 1979; Kunze 1989; Claßen-Bockhoff 2000, 2001; Stützel and Trovó 2013).

An inflorescence is a shoot system that bears flowers. A single axis bearing flowers is a simple inflorescence. Examples are racemes, spikes, simple umbels, and simple capitula (Weberling 1989, p. 207). When the flowers are replaced by axes with the same branching patterns as the simple inflorescence, the result is a compound inflorescence, and the individual branches are called partial inflorescences (Weberling 1989).

There are two main types of inflorescences: monopodial and sympodial (Weberling 1989). In Troll's system, monopodial inflorescences are called synflorescences. These inflorescences have a single main growing point. The inflorescences of the Zingiberales are monopodial synflorescences. In the Zingiberales, the terms "inflorescence" and "synflorescence" refer to the same structure. In sympodial inflorescences, the inflorescence apex terminates in a flower or flower cluster and growth of the inflorescence continues from a lateral bud. An example is the anthoclades of the Solanaceae (Danert 1958; Child 1979; Weberling 1989, pp. 285–287).

Synflorescences may be either monotelic (one ended) or polytelic (many ended; Troll 1964; Weberling 1965, 1983, 1989). In a monotelic synflorescence, each cluster of flowers is determinate and ends in a flower. In polytelic synflorescences, the flower clusters are indeterminate and lack a terminal flower.

The synflorescences of the Zingiberales are polytelic, so we will restrict our further discussion to this type. Synflorescences are composed of florescences, the basic repeating unit of the synflorescence. A florescence is a flowering axis whose structure is repeated throughout the synflorescence. Florescences bear lateral units (partial florescences) that may be either single flowers or groups of flowers.

When a florescence terminates the main axis of the plant, it is called the main florescence. A florescence borne on a lateral axis is a coflorescence. A synflorescence is thus a system of florescences (main and co-) collected together to form an inflorescence.

The branches below the main florescence repeat the structure of the synflorescence as a whole and are known as enriching branches (paracladia). Enriching branches increase the number of flowers over those in the main florescence. In most cases, enriching branches bear a variable number of bracts, but in *O. maxillarioides*, they bear only a prophyll and two bracts below the florescence (Kunze 1986). Kunze (1986) proposed the term "special paracladia" for enriching branches like this, which have a fixed number of elements.

In the Zingiberales, as in most monocotyledons, the first leaf (prophyll, PO:0009042) on each enriching branch lacks a blade (it is a scale leaf, PO:0006003) and is sterile. In most monocotyledons, the prophyll is two keeled, perhaps because of pressure on the developing prophyll, which is wedged between two axes.

In the Zingiberales, the partial florescences are cincinni (monochasial, PO:0030132; cymes, PO:0030126) or, in families like the Lowiaceae, single flowers derived from cincinni. A cincinnus is a lateral branch system in which each axis terminates in a flower and bears a single bract bearing a new flower in its axis. Each cincinnus is subtended by a bract, a scale leaf that occurs in an inflorescence. The bracts borne on the florescence axis are called the main, primary, or first-order bracts (Holttum 1950) or floral bracts (Jenjittikul and Larsen 2002; Leong-Škorničková et al. 2014). We will refer to them as the floral bracts in the rest of this article. In the Lowiaceae, the partial florescence is reduced to a single flower and its subtending floral bract (Kunze 1986).

In most Zingiberales, the vegetative shoots terminate in a synflorescence and growth is continued by renewal shoots originating in the axil of a lower leaf (Holttum 1955). The renewal shoots usually grow for a period of time and then terminate in a synflorescence. Additional renewal shoots are produced beneath the new synflorescence (Holttum 1955).

Floral Terminology

In *Orchidantha*, the terms "adaxial" and "posterior" refer to the same side of the flower, as do the terms "abaxial" and "anterior" (fig. 1). At initiation, the adaxial/posterior side of the flower backs onto the florescence axis, while the abaxial/anterior side of the flower faces away from this axis (fig. 1). In the remainder of this article, we will refer to the adaxial/posterior side of the flower as posterior and the abaxial/anterior side as anterior, in keeping with the terminology used by Kirchoff and Kunze (1995). In all polar views in this article, the anterior side of the flower is the side at the bottom of the photograph.

After initiation, the flowers rotate 180° (resupination) so that the largest petal, the labellum, is displayed at the bottom of the flower (fig. 2). The labellum is initiated adjacent to the florescence apex, but as the flower flips over, this petal is displayed at the bottom of the open flower (fig. 2).

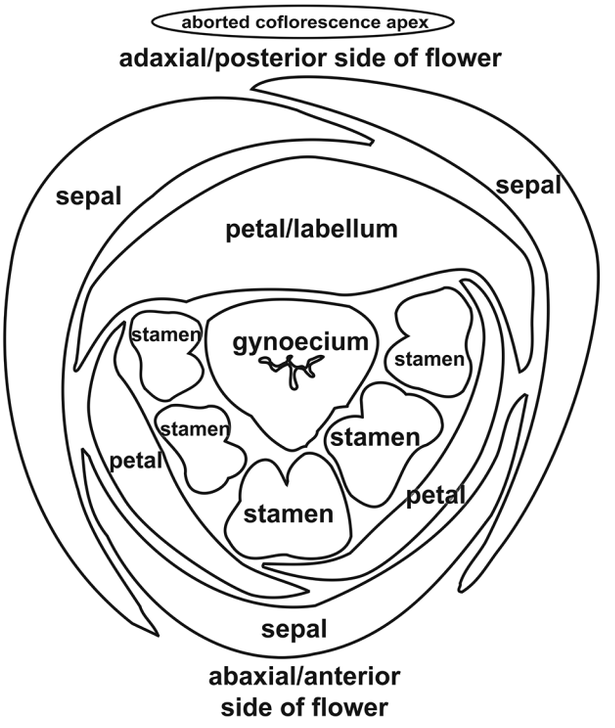

Fig. 1 *Orchidantha* floral diagram based on a cross section of a flower bud of *O. maxillarioides*.

Results

Organography

Orchidantha chinensis is a small, ca. 70-cm rhizomatous herb that grows sympodially, with occasional lateral branching (fig. 3*A*, 3*C*). The leaves are initially distichous or nearly distichous (fig. 3*D*, inset) but become oriented to one side as they mature, perhaps because of the rhizome's growth through the soil (fig. 3*D*). Vegetative buds form in the axil of every foliage leaf or alternating foliage leaves, depending on the shoot. Each of these buds presumably has the potential to grow out and produce a vegetative branch (fig. 3*C*). Immediately below the terminal synflorescence, one or two of the buds grow out to produce renewal shoots (figs. 4*A*, 5). The renewal shoots continue the growth of the rhizome.

The inflorescence of *O. chinensis* is a polytelic synflorescence that lacks a main florescence (fig. 5). The synflorescence apex aborts after forming two enriching branches (figs. 4*A*, 4*B*, 5) without forming a main florescence. Each enriching branch (paracladium) bears an adaxial prophyll (the first bract of the paracladium) followed by two additional bracts (figs. 4, 5) and terminates in a coflorescence. The coflorescence consists of a single floral bract subtending a single flower and an aborted coflorescence apex (fig. 5). One or both bracts subtend buds

Fig. 2 Resupinate mature flower of *Orchidantha chinensis*. From W. J. Kress, used with permission.

that have the potential to develop into higher-order enriching branches (paracladia) of the synflorescence (figs. 4*D*, 5, blue branches). In our material, the larger of these buds was borne in the axil of the upper bract and, upon dissection, possessed the same organs as the expanded enriching branch (fig. 5, cf. blue and black branches). We did not encounter any inflorescences in which these buds produced open flowers.

The flowers are solitary in the axil of the floral bract (fig. 5). The flower parts are arranged in threes, with a perianth (PO:0009058) of three sepals (PO:0009031) and three petals (PO:0009032), five stamens (PO:0009029), and a three-parted gynoecium (PO:0009062; figs. 1, 2). The sepals are larger than the petals and persist on the fruit (PO:0009001; figs. 2, 3*B*). The three petals are unequal in size. Two are smaller, and one, the labellum, is much larger (fig. 2). A single member of the inner androecial whorl, the posterior stamen, is missing, resulting in five mature stamens. The gynoecium is trimerous, syncarpous, and trilocular, with axile placentation and numerous ovules (PO:0020003) per locule (PO:0025266). The ovary (PO:0009072) is inferior. The fruit tapers into a sterile beak, a prolongation of the inferior ovary that persists on the fruit (fig. 3*B*).

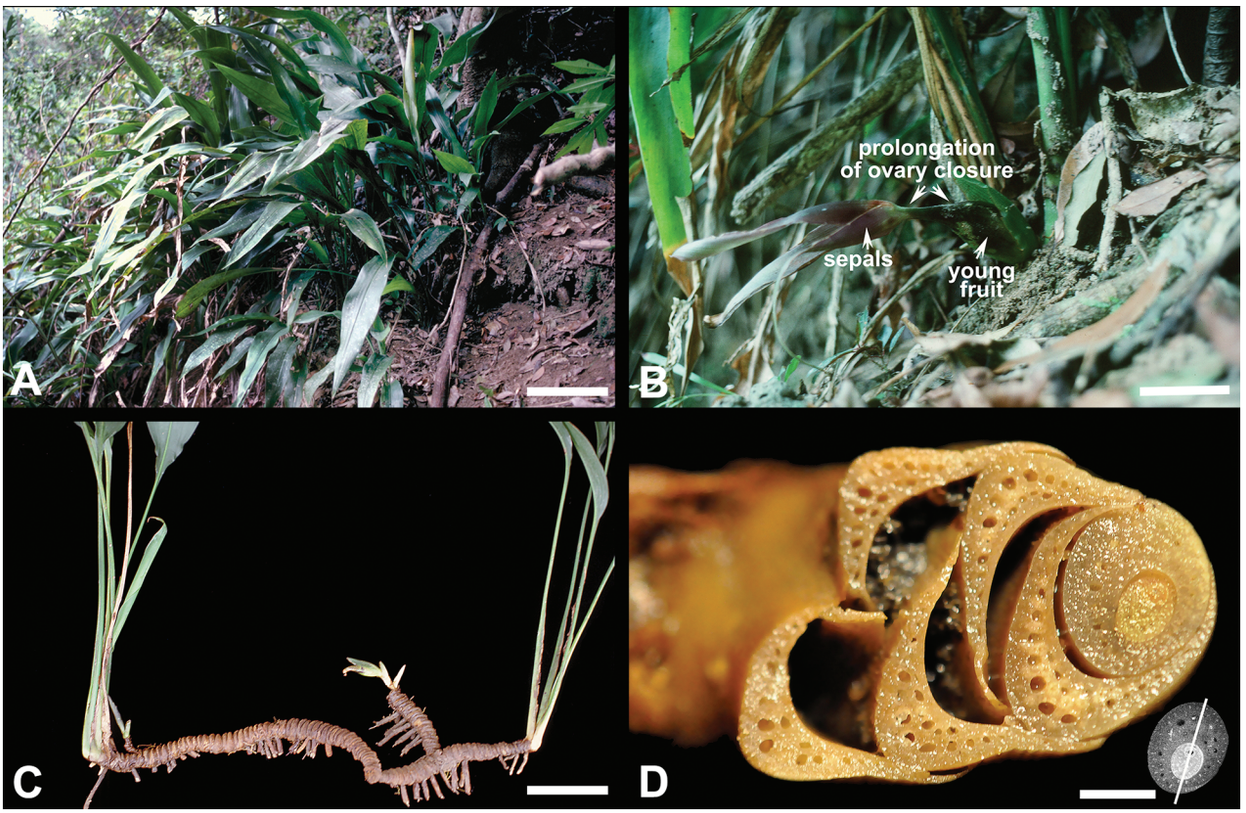

Fig. 3 *Orchidantha chinensis*. *A*, Whole plant. Scale bar = 200 mm. *B*, Young fruit, showing persistent calyx and prolongation of the closure of the ovary. Scale bar = 50 mm. *C*, Rhizome with axillary branching. Scale bar = 100 mm. *D*, Cross section of growing shoot, showing reorientation of leaves as the rhizome presses through the soil. *Inset*, Cross section, showing approximate distichous insertion of leaves. Line indicates plane of distichy. Scale bar = 5 mm.

Development

Two second-order enriching branch buds form in the axils of the bracts below each coflorescence (figs. 4*D*, 5, 6*A*). Each bud first initiates an adaxial prophyll (fig. 6*B*), followed by two bracts, only one of which is shown in the figures (fig. 6*B*–6*D*). The coflorescence, which consists of a single floral bract subtending a solitary flower and an aborted coflorescence apex, forms next (fig. 6*E*, 6*G*, 6*H*). The floral bract is the fourth bract of the enriching branch. The coflorescence apex aborts soon after this bract is initiated (fig. 6*F*–6*H*), resulting in a small stub of tissue adjacent to the single flower (fig. 6*F*).

Flower development begins with the formation of the floral apex in the axil of the floral bract (fig. 6*G*). As it forms, the floral apex separates from the coflorescence apex (fig. 6*G*, 6*H*). The first and second sepals form on the posterior edges of the flower primordium (fig. 6*G*, 6*H*). The first sepal (fig. 6*G*, 6*H*, arrows) may appear on either side of the flower (cf. fig. 7*A*). The anterior sepal is initiated last (fig. 7*B*) and remains smaller than the posterior sepals throughout development (figs. 7*C*–7*E*, 8*B*, 8*C*, 8*E*, 8*G*, 8*H*).

The three petals are formed at approximately the same time as or even slightly before the third sepal (fig. 7*B*). It was not possible to determine the sequence of petal formation because *O. chinensis* goes dormant at about this time (fig. 7*A*, 7*B*) in South China, making it difficult to find intermediate developmental stages. Soon after initiation and throughout early development, the three petal primordia (PO:0000021) are approximately the same size (figs. 7*B*–7*F*, 8*D*, 8*F*, 9*D*, 9*F*). Sometime later, the posterior petal enlarges to form the labellum, which is approximately four times the length of the anterior petals in the mature flower (fig. 2). Soon after initiation, all the petals develop a small keel (figs. 7*G*, 7*H*, 8*D*, 8*F*), which does not persist past the early developmental stages (fig. 9*D*, 9*F*).

Growth below and between the petals creates a shallow cup at the center of the flower (fig. 7*B*, 7*C*). The androecium (PO:0009061) and gynoecium form from the margins of this cup. The three members of the outer androecium, the outer stamens, form between the petals (fig. 7*C*, arrows). The two inner stamens form from the inner margins of the cup, opposite the two anterior petals (fig. 7*D*, 7*E*, arrows). The third member of the inner androecium is not initiated. If it were, it would appear directly interior to the posterior petal.

Growth of the floral cup below the point of stamen attachment deepens the cup and prepares for gynoecial initiation (fig. 7*F*). Three gynoecial primordia arise on the inner margins of the cup, opposite the outer stamens (figs. 7*F*–7*H*, 8*A*). These primordia become conduplicate as they enlarge (figs. 7*G*, 8*D*, 8*F*, 9*B*–9*F*). They eventually fuse to form the inferior ovary, below, and the style and stigma, above (fig. 9*E*, 9*F*).

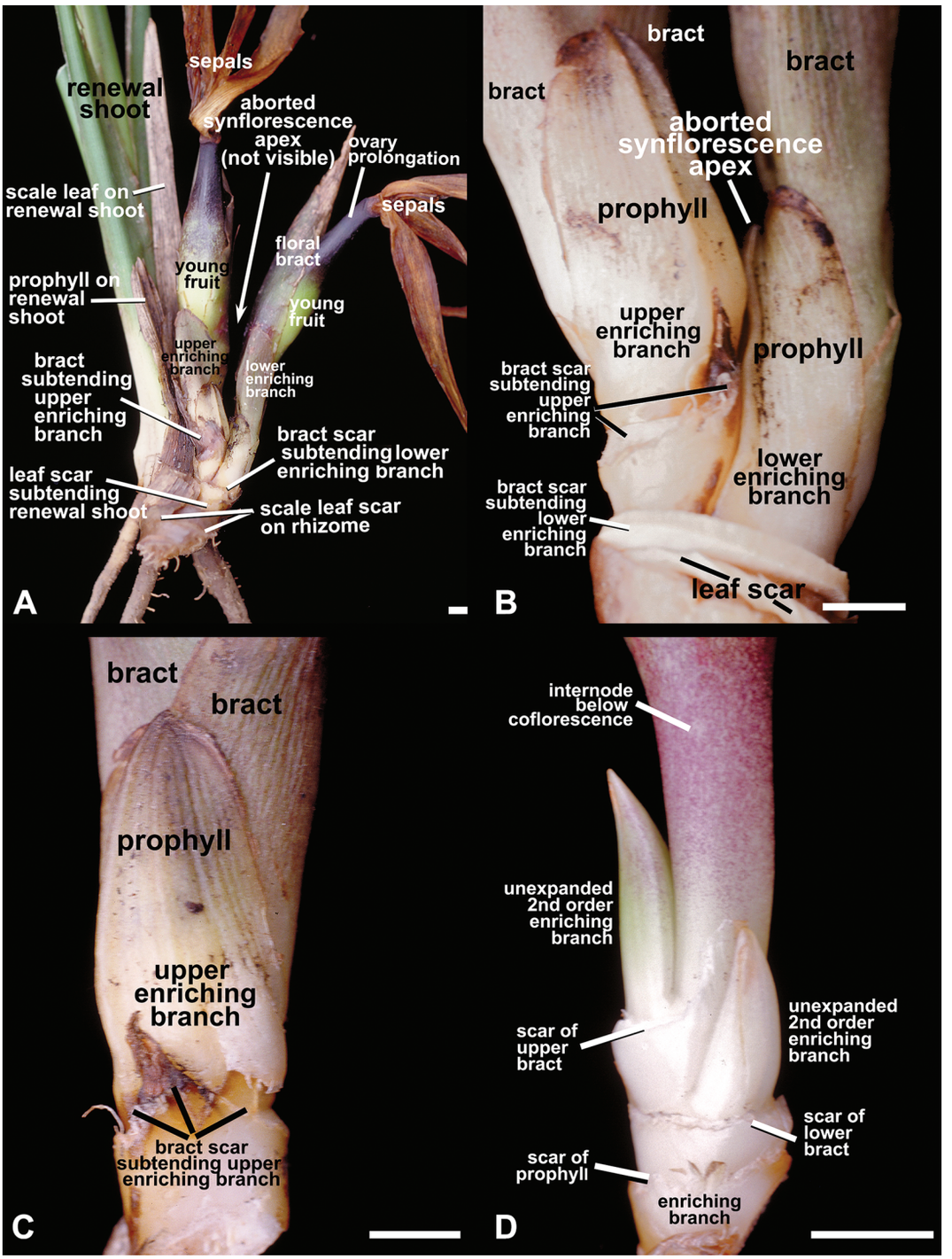

Fig. 4 *Orchidantha chinensis*. *A*, Two flowers/fruits in a terminal synflorescence (*right*), with axillary renewal shoot arising below (*left*). *B*, Two enriching branches of a terminal synflorescence. The synflorescence apex aborts. *C*, Adaxial view of the left enriching branch of the synflorescence in *B*. A small part of the bract subtending the enriching branch is visible as a brownish triangle at the bottom of the image. This triangle of tissue is also visible in *B*. *D*, Enriching branch of a synflorescence with the prophyll and two middle bracts removed to reveal the second-order enriching branch buds. Scale bars = 5 mm.

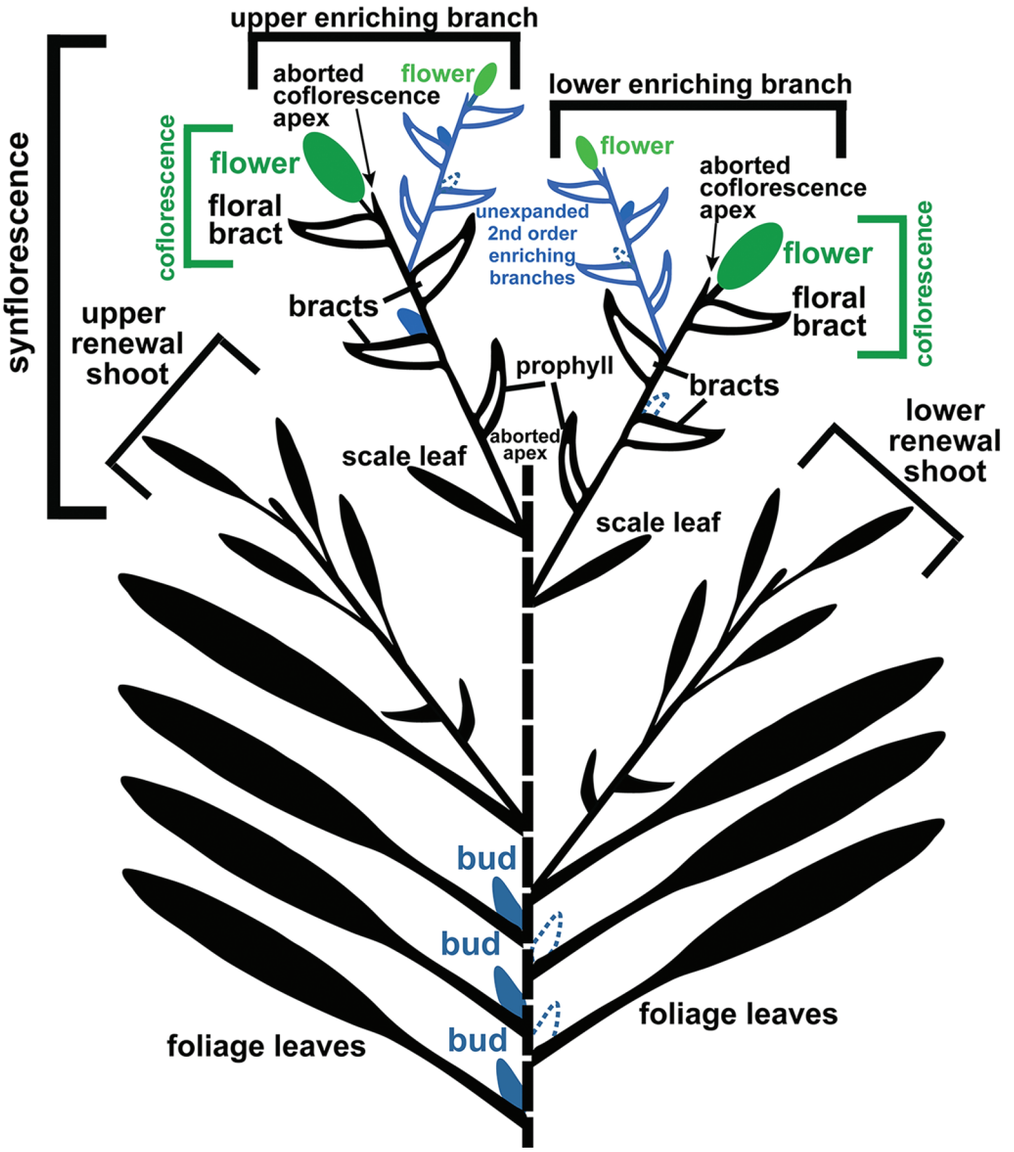

Fig. 5 Diagram of the shoot system and synflorescence of *Orchidantha chinensis*. All axes, dashed or solid, have been lengthened to reveal their structure. Buds shown with dashed blue lines were not present in all shoots. The second-order enriching branches (blue) were present in the bud. We did not observe any expanded second-order branches.

Careful observation discerns a pattern of sequential initiation in the androecium and gynoecium. The anterior outer stamen is formed first, followed sequentially by the two posterior outer stamens (fig. 7*D*, 7*E*). The two anterior inner stamens are also initiated in a spiral sequence, as are the three gynoecium primordia (fig. 7*F*). The direction of the initiation sequence is almost certainly related to the handedness of the flower, which is determined by the first-formed sepal (figs. 6*H*, 7*A*).

There is variability in both the shape of the flower primordium as a whole and the shape and relative size of the gynoecial primordia. In some apexes, the flower primordium is almost radially symmetrical, and all the floral organs are clearly visible (fig. 8*F*). In others, the flower is laterally compressed, and the anterior gynoecial primordium is smaller than the others (fig. 7*G*). The gynoecial members may all be distally conduplicate (figs. 8*B*, 8*F*, 9*B*), only two may be conduplicate (fig. 9*C*), or none may (fig. 9*A*). The anterior gynoecial primordium may be clearly visible (figs. 8*B*, 8*F*, 9*B*), partially hidden beneath the inner stamens (fig. 9*C*), or completely hidden (figs. 7*H*, 8*D*, 9*A*). The flowers with the greatest lateral compression are the ones where the gynoecial member is least visible (figs. 7*H*, 8*D*).

Discussion

Inflorescence Structure

As Weberling (1965) and Claßen-Bockhoff (2000) point out, there are two levels of inflorescence structure. The first level is

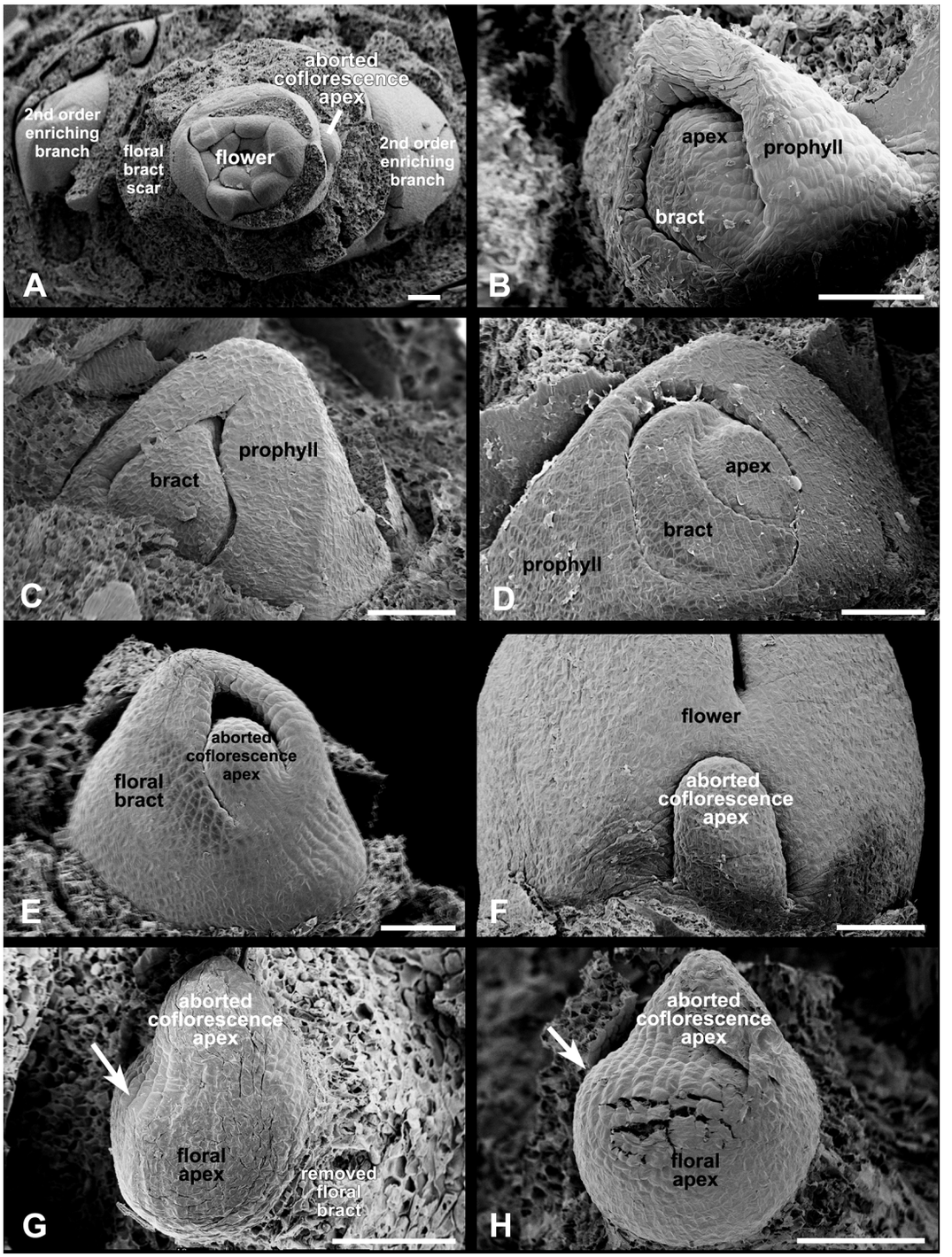

Fig. 6 Enriching branch and early flower development in *Orchidantha chinensis*. *A*, First-order enriching branch terminating in a one-flowered coflorescence and aborted apex. *B*, Lower of two second-order enriching branches (paracladia). *C*, Upper of two second-order enriching branches (paracladia). *D*, Further development of the lower of the two second-order enriching branches (paracladia). *E*, Coflorescence with abortive apex. *F*, Flower adjacent to abortive coflorescence apex. *G*, Floral apex at the time of first sepal (arrow) initiation. Compare with figure 7*A*, which shows a flower with the first sepal initiated on the opposite side of the flower. *H*, Later stage of first sepal (arrow) initiation. The floral apex has enlarged in preparation for initiation of the second sepal on the opposite side of the flower. Floral bract removed. Scale bars = 100 μm.

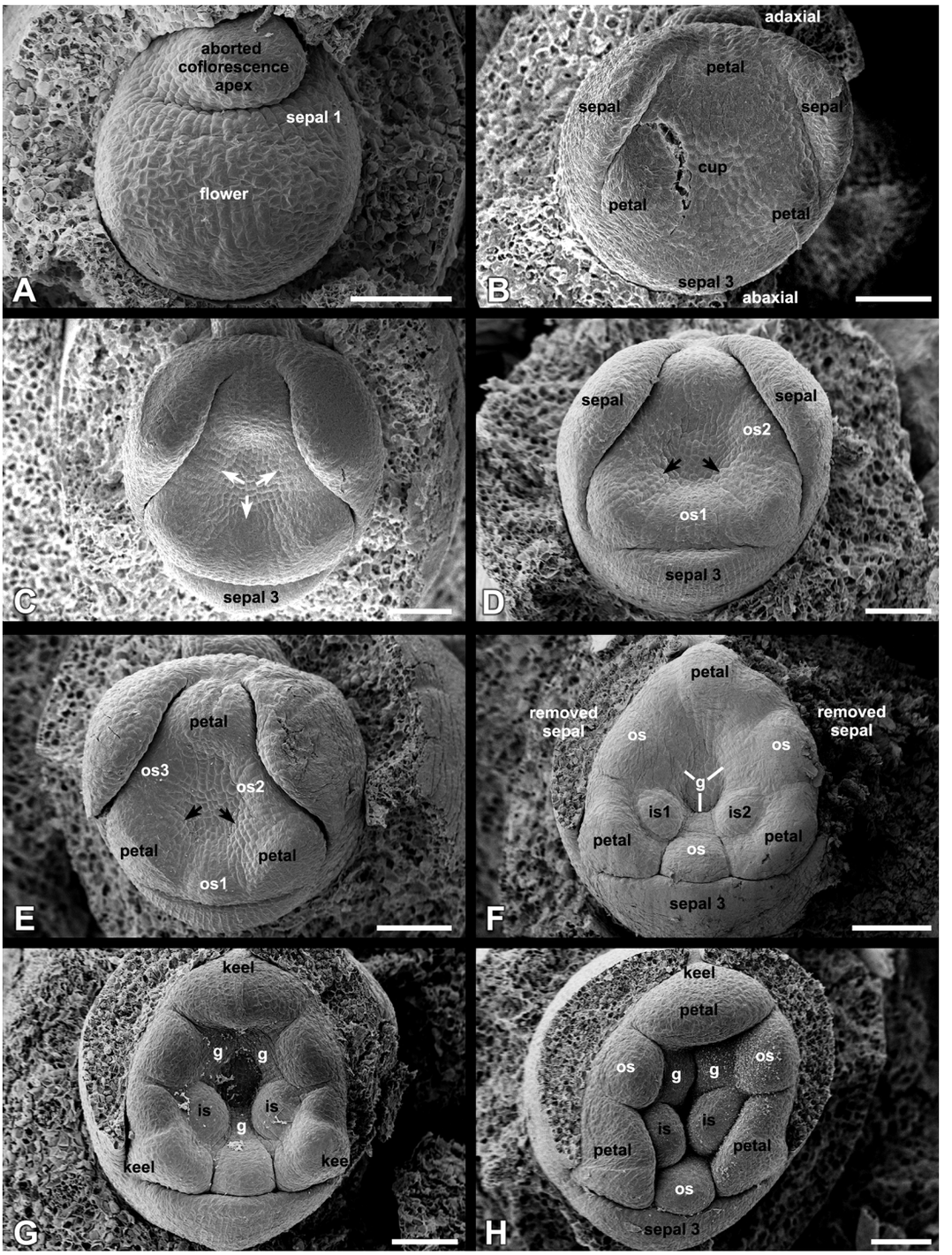

Fig. 7 Flower development in *Orchidantha chinensis*, sepal through gynoecial initiation. *A*, Enlargement of the floral apex and initiation of the first sepal. Floral bract removed. *B*, Petal initiation and beginning of the formation of the floral cup. Initiation of the third sepal lags petal initiation. *C*, Continued formation of the floral cup and early stages of outer androecial initiation (arrows). The third sepal is present but is smaller than the other two sepals. *D*, Continued development of the outer stamen (os1, os2) and early initiation of the two anterior inner stamens (arrows). No posterior inner stamen is initiated. *E*, Slightly oblique view of the flower in *D*, more clearly showing the inner androecial initiation (arrows), the initiation of the outer stamens (os1–os3), and the lack of a posterior inner stamen. *F*, Early gynoecial initiation (g) with well-developed outer stamens (os) and inner stamens (is1, is2). Rapid sequential initiation of both the inner stamens and the gynoecial primordia can be seen. There is still no posterior inner stamen. Posterior sepals removed. *G*, Later stage in the formation of the gynoecial primordia (g), showing two of them becoming slightly conduplicate. Posterior sepals removed. is = inner stamen. *H*, Further development of the gynoecial primordia (g) in the same flower as in figure 8*A*. The flower is laterally compressed. Only two gynoecial primordia are visible because of lateral compression of the flower and the position of the inner stamen primordia (is). Posterior sepals removed. os = outer stamen primordium. Scale bars = 100 μm.

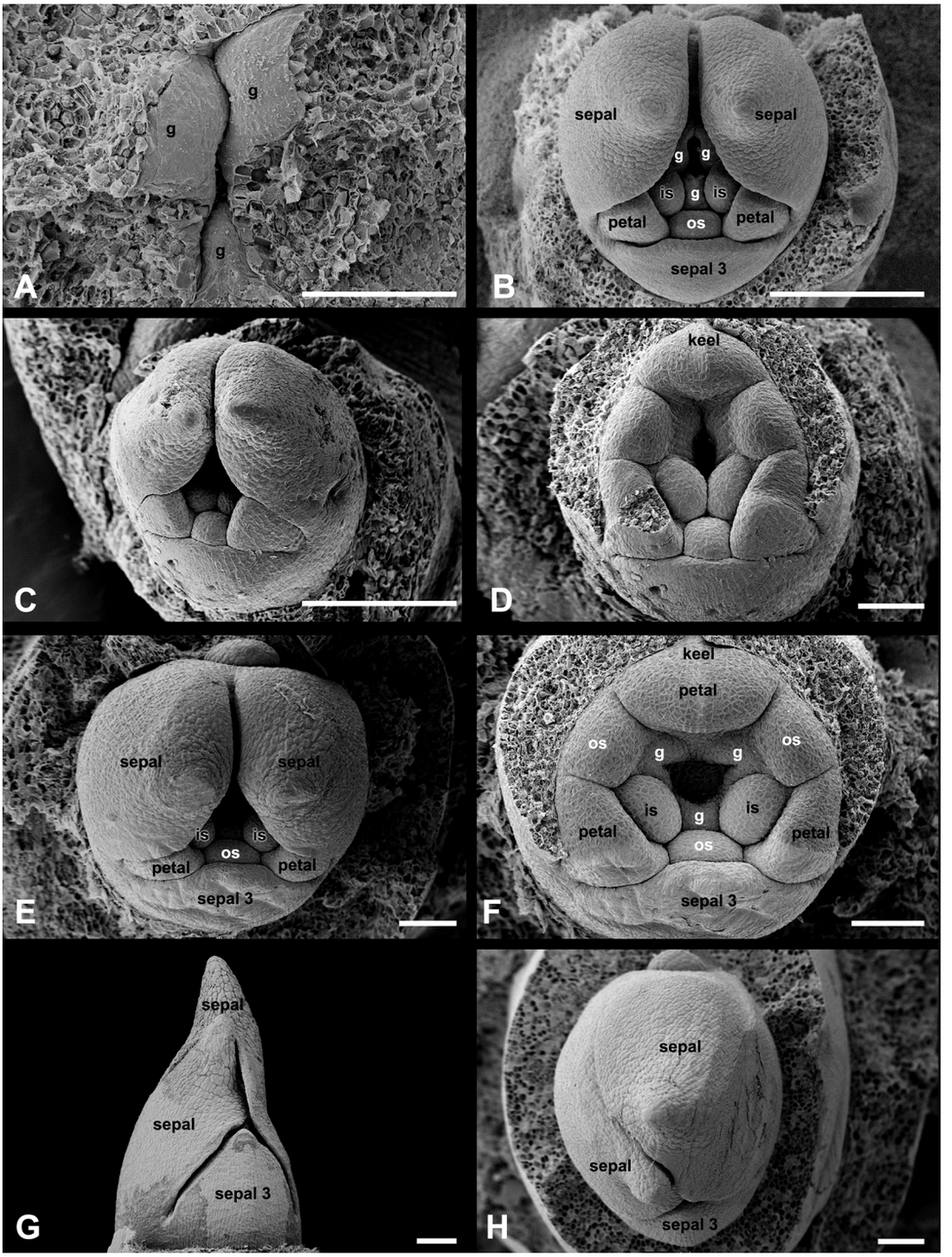

Fig. 8 Gynoecial development and developmental variations in *Orchidantha chinensis*. *A*, Early gynoecium (g) formation in the same flower as in figure 7*H*. The floral cup is closed because of the lateral compression of the flower. Only two of the gynoecial primordia are (slightly) conduplicate. All other floral organs removed. *B*, Gynoecial initiation (g) in a flower with an open floral cup. The difference in size of the three sepals is apparent. Neither the inner stamen (is) nor the outer stamen (os) obscures the gynoecial primordia in this type of flower. *C*, Slightly oblique view of the same flower as in *D*, showing the relationships of the parts before removal of the posterior sepals. *D*, Gynoecial initiation in the same flower as in *C*. The floral cup is partially open (cf. *F*), and two conduplicate gynoecial primordia are visible. The flower is slightly laterally compressed. Posterior sepals removed. *E*, Slightly oblique view of the same flower as in *F*, showing the relationships among the parts. is = inner stamen; os = outer stamen. *F*, Gynoecial initiation in the same flower as in *E*. The floral cup is open, and three conduplicate gynoecial primordia (g) are visible because the inner stamens (is) do not overlap the floral cup. The flower is not laterally compressed. Posterior sepals removed. os = outer stamen. *G*, Lateral view of the same flower as in *H* and figure 9*A*. All floral organs have been initiated, and the sepals have closed over the flower. The posterior sepals are much larger than the anterior sepal (sepal 3). *H*, Polar view of the same flower as in *G* and figure 9*A*, showing the relative sizes of the sepals and their pattern of overlap (aestivation). The aborted floral apex can be seen on the posterior side of the flower, at the top of the photograph. Scale bars = 100 μm.

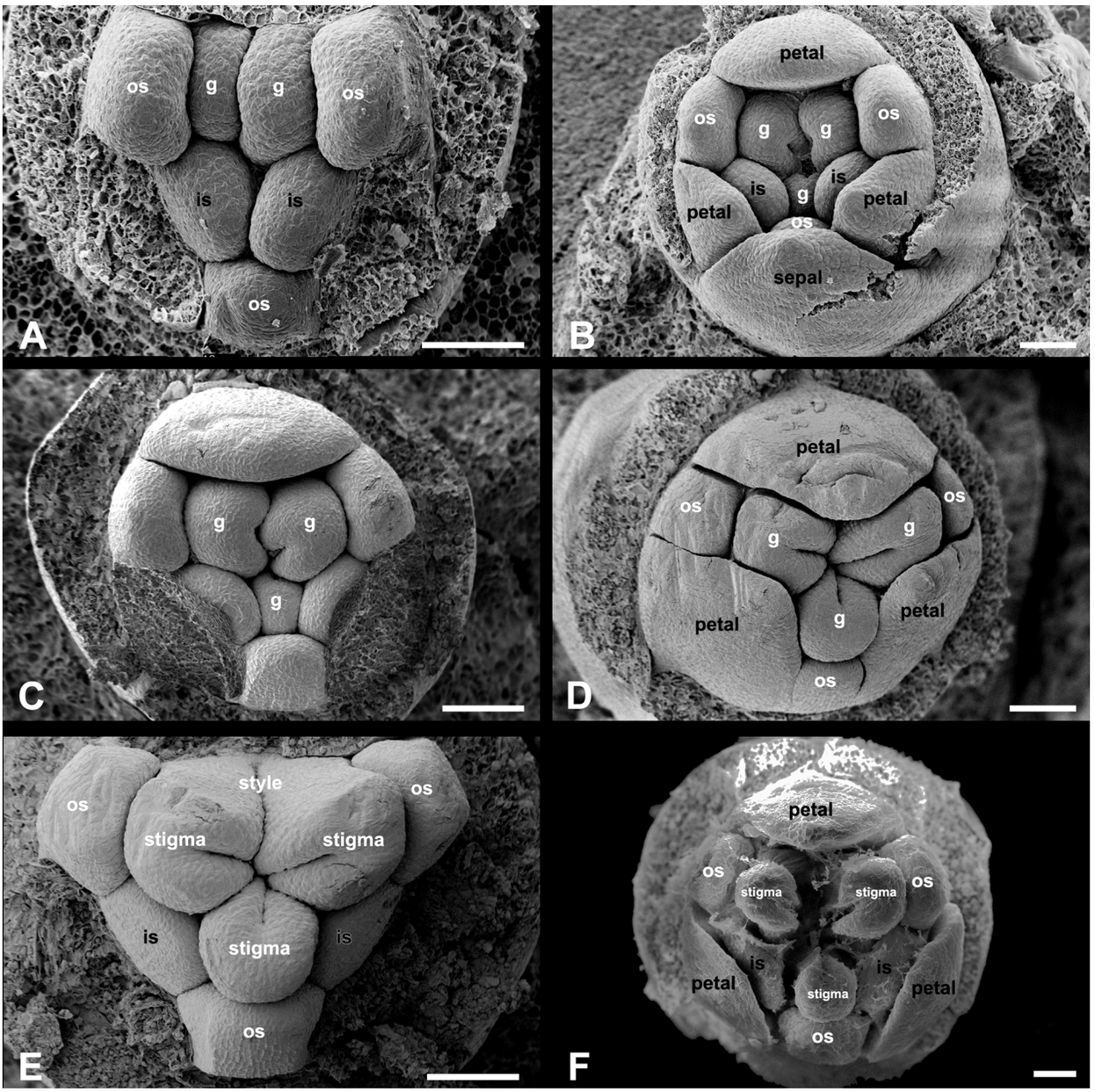

Fig. 9 Gynoecial development in *Orchidantha chinensis*. *A*, Outer stamen (os) and inner stamen (is) and two slightly conduplicate gynoecial primordia (g) in the same flower as in figure 8*G* and 8*H*. Sepals and petals removed. *B*, Three conduplicate gynoecial primordia (g) in a flower with an open floral cup. The anterior sepal (labeled) is approximately the same size as the posterior petal (labellum), and the outer stamen (os) and inner stamen (is) are distinct. Posterior sepals removed. *C*, Flower at approximately the same stage as *B* but with only two of the gynoecial primordia (g) conduplicate. Posterior sepals and anterior petals removed. *D*, Later stage in gynoecial formation. All of the gynoecial primordia (g) are conduplicate as they begin to form the stigma and style. Sepals removed. os = outer stamen. *E*, Later formation of the style and stigma through the fusion of the three gynoecial primordia. Posterior sepals and anterior petals removed. is = inner stamen; os = outer stamen. *F*, All floral organs present (sepals removed) at a late stage of organogenesis. There was considerable shrinkage of this flower during freeze-drying. is = inner stamen; os = outer stamen. Scale bars = 100 μm.

the branching structure of the vegetative body. The second is the structure of the inflorescence, as distinct from the vegetative plant body. However, in some cases there may not be a clear distinction between the vegetative and the reproductive regions of the plant. For instance, Grimes's (1999) critique of Troll's (1964) terminology is partially based on the continued growth of the inflorescence apex beyond the floral region to produce the next set of leaves and flowers. This same type of growth

occurs in *Dimerocostus strobilaceus* (Costaceae) and in many members of the Strelitziaceae (Maas 1972; Cron et al. 2012; B. K. Kirchoff, personal observation).

Inflorescences have a modular structure. They are composed of repeated units that are often hieratically arranged in complex ways (Grimes 1992; Sell and Cremers 1992; Stützel and Trovó 2013). This modular structure is a special case of the modular growth that characterizes most plants (White 1984; Hallé et al. 1986).

In plants where the shoot apex terminates in a synflorescence, vegetative renewal shoots arise in the axils of leaves below the synflorescence and continue the growth of the plant. In the Zingiberales, these renewal shoots also terminate in synflorescences, with higher-order renewal shoots arising below them. The renewal shoots are thus part of the shoot system that forms the inflorescence, though there is no terminology to adequately deal with this fact. The number of foliage leaves produced on a renewal shoot varies widely among shoots and almost certainly among species.

With two detailed investigations of inflorescence structure and the data from taxonomic descriptions (see below), enough species have now been investigated that the inflorescence of *Orchidantha* can be said with confidence to be a polytelic synflorescence that lacks a main florescence. It is a truncated polytelic synflorescence, as originally described by Kunze (1986). The main florescence never forms because the synflorescence apex, that is, the apex of the main shoot, aborts before it is produced (fig. 4*A*, 4*B*). Each enriching branch (paracladium) of the synflorescence bears three bracts and terminates in a coflorescence. The four bracts commonly described in the taxonomic literature are a prophyll followed by two middle bracts and the single floral bract of the coflorescence (Nagamasu and Sakai 1999; Leong-Škorničková 2014; Leong-Škorničková et al. 2014; Zou et al. 2014, 2017; Poulsen and Leong-Škorničková 2017). The floral bract subtends a single flower. The coflorescence apex may produce additional rudimentary bracts, but it aborts soon after producing the floral bract (fig. 6*F*; Kirchoff and Kunze 1995).

Kunze (1986) was the first to explicitly recognize the structure of the inflorescence through his description of *O. maxillarioides*. Kirchoff and Kunze (1995) verified this description and provided a description of flower development in this species. Older interpretations of the inflorescence are discussed more fully in Kirchoff and Kunze (1995). Since Kirchoff and Kunze (1995), inflorescence structure has been described in several other species as part of new species descriptions.

Nagamasu and Sakai (1999) describe the inflorescence of *O. inouei* and investigate the structure of its richly branched inflorescence. They report that, in the lower part of the synflorescence, both middle bracts subtend higher-order enriching branches (paracladia), while in the upper part, only the upper bract does (fig. 10). This produces branched enriching branches (paracladia) at the base of the synflorescence and sympodially branched axes distally (Nagamasu and Sakai 1999). This sympodial branching pattern may have given rise to Holttum's (1970) somewhat confusing description of the inflorescence as a series of monochasial cymes. It must also certainly be responsible for Larsen's description of the inflorescence as consisting of "sympodially connected paracladia each producing a single flower" (Larsen 1998, p. 275).

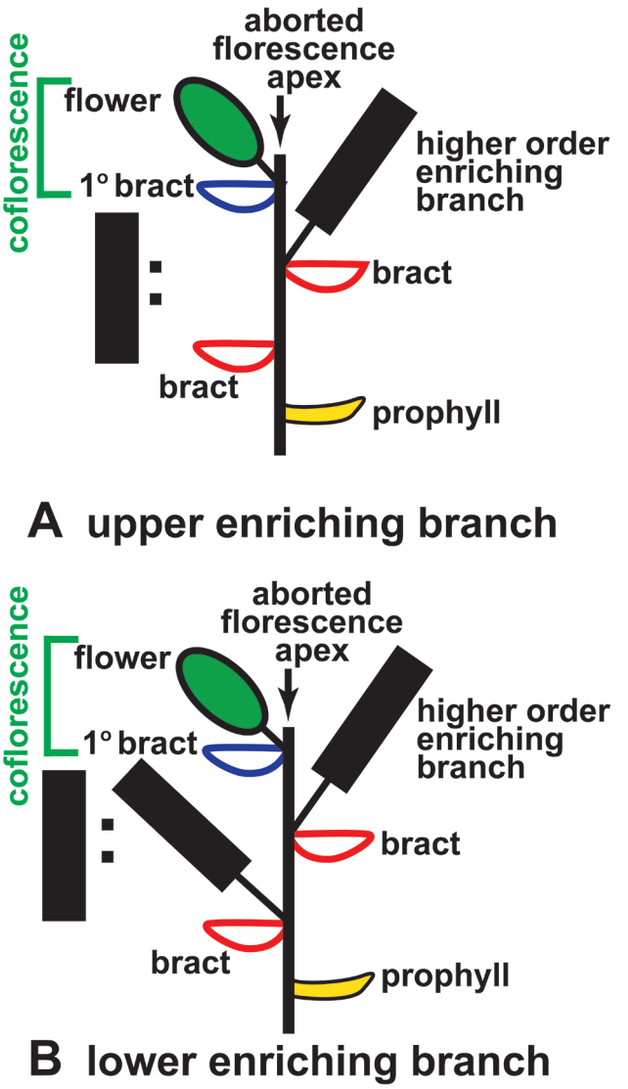

Fig. 10 Enriching branch (paracladium) structure in *Orchidantha inouei* after Nagamasu and Sakai (1999). The enriching branches are hierarchically nested, as indicated by the relationship between the boxes on the left of the image and the expanded diagrams on the right. The box on the left represents the whole structure shown to the right, on the other side of the colon. The repetition of the box represents the repetition of the whole structure at the next hierarchical level. *A*, Enriching branches (paracladia) higher in the synflorescence bear higher-order enriching branches only in the axil of their upper bracts. This is sympodial branching, as described in Nagamasu and Sakai (1999). *B*, Enriching branches (paracladia) lower in the synflorescence bear higher-order enriching branches in the axil of both bracts. This produces a branched synflorescence.

This pattern of basal branching and distal sympodia has been found in several other species. Pedersen (2001) describes four new species of *Orchidantha* from Sabah (*O. suratii*, *O. sabahensis*, *O. quadricolor*, and *O. grandiflora*) and reports that their inflorescence structure agrees with that found by Nagamasu and Sakai (1999). Zou et al. (2014) found the same pattern in *O. insularis*.

On the basis of these observations, one of us (B. K. Kirchoff) reinvestigated inflorescence branching in *O. maxillarioides* using the same collections but not the same inflorescences as studied by Kirchoff and Kunze (1995). He found indications of this same pattern, though the enriching branches available for study had only three orders of branching. By the third order, the first of the middle bracts was sterile or subtended a small bud, while the second of the middle bracts subtended a higher-order enriching branch. This is the same pattern as that described by Nagamasu and Sakai (1999).

The only other family in the Zingiberales where the polytelic synflorescence lacks a main florescence is the Strelitziaceae. Of the three genera in the family, both *Ravenala* (one species) and *Strelitzia* (five species) lack a main florescence. Flowers are produced only on lateral enriching branches that terminate in coflorescences (Fisher 1976; Calley et al. 1993). These coflorescences have the structure of a simple thyrse: the axis of the coflorescence bears lateral bracts that subtend cincinni. The main axis of these plants continues to grow and produce leaves (fig. 11). In other species of *Strelitzia* (*S. reginae* and *S. juncea* are examples), the coflorescences are further reduced to a single bract that subtends a lateral cincinnus.

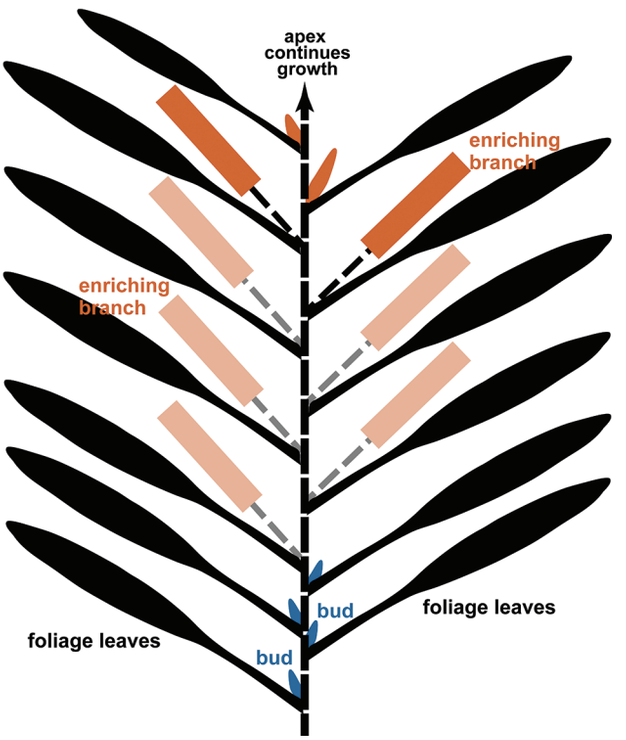

Fig. 11 Shoot/synflorescence structure in *Strelitzia nicolai* (Strelitziaceae). Once a shoot becomes fertile, every leaf subtends an enriching branch. The shoot apex continues to grow and does not produce a main florescence. The enriching branches bear a prophyll and three sterile bracts and terminate in a coflorescence of three or four floral bracts, each subtending a cincinnus of flowers. At most, two enriching branches will bear flowers at any one time (dark rectangles), while the older branches bear fruits or have fallen (light rectangles).

The inflorescence of *Phenakospermum* (one species) consists of a single main florescence with no enriching branches or coflorescences (Kress and Stone 1993; Kirchoff 2003; Cron et al. 2012). *Phenakospermum* is monocarpic. The main axis dies after flowering and growth continues from a renewal shoot produced at the base of the main shoot.

Given these facts, the similarities and differences in inflorescence structure in the Lowiaceae and Strelitziaceae can be summarized as follows. In both *Orchidantha* and all members of the Strelitziaceae, except for *Phenakospermum*, the polytelic synflorescence lacks a main florescence and the flowers are produced from coflorescences. In the other species of *Strelitzia*, the coflorescences are reduced to a single bract. In the Strelitziaceae, the bracts subtend cincinni, whereas in *Orchidantha*, they subtend single flowers. In *Orchidantha*, additional flowers are produced from higher-order enriching branches (paracladia) that rise below the coflorescences, while in the Strelitziaceae, no higher-order enriching branches are ever produced. The inflorescence of *Phenakospermum* is the most different from that of *Orchidantha*. The inflorescence of *Phenakospermum* consists of a single terminal main florescence and lacks both enriching branches and coflorescences.

Which of these characters are uniquely derived (synapomorphies) depends on the placement of the Lowiaceae in the phylogeny of the order, which is discussed more fully below. If we accept Cron et al.'s (2012) phylogenetic analysis of the Strelitziaceae, which is predicated on the placement of the Lowiaceae as sister to the Strelitziaceae, then the lack of a main florescence in *Orchidantha* and most species of the Strelitziaceae is a uniquely derived character (synapomorphy) of the (Lowiaceae, Strelitziaceae) clade. The reduction of the coflorescence from many cincinni to a single cincinnus is consequently a uniquely derived character of the ((*S. reginae, S. juncea*), (*S. alba, S. caudata*)) clade, and *Phenakospermum* possesses a main florescence as a uniquely derived character.

Flower Structure and Development

Inflorescence and flower development are very similar in *O. chinensis* and *O. maxillarioides* (Kirchoff and Kunze 1995). The central difference in inflorescence development is the initiation of additional bracts beyond the single floral bract in the coflorescence of *O. maxillarioides* and the lack of these bracts in *O. chinensis*. Other than that, we found no significant differences in inflorescence development between the two species.

Flower development differs in the two species in that there is a common primordium that unites the posterior petal (labellum) and two outer androecial members in *O. maxillarioides* (Kirchoff and Kunze 1995), while this common primordium is lacking in *O. chinensis*. In *O. chinensis*, the posterior petal and posterior outer stamens are initiated independently. However, there are some important caveats to this conclusion. First, Kirchoff and Kunze (1995) were working with very limited material, and only one of their images unequivocally shows the presence of the common primordium (Kirchoff and Kunze 1995, fig. 12). Given the variability described in *O. chinensis*, it is possible that this image represents a variation in normal floral development, not the common pattern in this species. Second, at the time of petal initiation, the margins of the floral cup are beginning to grow upward in preparation for the formation of the gynoecium. This upward

growth makes it extremely difficult to determine whether two adjacent primordia are congenitally fused or whether their close proximity is due to the upward growth of the margins of the floral cup. Kirchoff and Kunze (1995) adopted the first interpretation, while we have accepted the second. The reported developmental difference between these two species may be purely one of semantics because of this difficulty.

It is also important to note that we have described flower development in *O. chinensis* much more thoroughly than was possible in *O. maxillarioides*, and so there is little basis for detailed comparisons. Because of the greater amount of material available for *O. chinensis*, we were able to document variability in the shape of the flower primordium and in the shape and relative size of the gynoecial primordia. However, none of this variability affected the overall pattern or sequence of organ formation. It is possible that the lateral compression that is associated with this variability was caused by dissection damage and is not a normal part of flower development. However, normal dissection does not usually result in compression, and it is equally possible that the compression is the result of pressure on the developing inflorescence exerted by the surrounding tissues. Our more than 30 years of dissection experience lead us to suspect the latter.

As in *O. maxillarioides*, the third sepal of *O. chinensis* is initiated much later than the first two sepals, at approximately the time of petal formation. This pattern of delayed initiation is also found in *Musa* (Musaceae) and *Phenakospermum* (Strelitziaceae; Kirchoff 2003, 2017) but not in *Heliconia* (Heliconiaceae; Kirchoff 2003; Kirchoff et al. 2009). The delayed initiation is not correlated with the orientation of the flowers at their time of initiation, which is similar in *Orchidantha*, *Musa*, and *Heliconia* but differs in *Phenakospermum*. This suggests that the delayed initiation of the third sepal could be a shared derived character (synapomorphy) that unites the Lowiaceae, Strelitziaceae, and Musaceae into a monophyletic group, as has been suggested in some phylogenetic analyses (Barrett et al. 2014).

Phylogenetic analyses have most commonly placed the Lowiaceae as the sister group to the Strelitziaceae, though Carlsen et al. (2018) have suggested that it may never be possible to unequivocally resolve the relationships among the four banana families (Musaceae, Strelitziaceae, Lowiaceae, and Heliconiaceae). One notable exception to the placement of the Lowiaceae as the sister group to the Strelitziaceae is Johansen's (2005) analysis of the phylogeny of *Orchidantha*, which included a phylogenetic analysis of the order. Johansen (2005) places the Lowiaceae at the base of the order, as the sister group of the other families. This conclusion is based on both molecular and morphological characters. The morphological characters were taken, with slight modification, from Kress et al. (2001). Johansen (2005) coded two floral characters differently from Kress et al. (2001). She coded the presence of the sixth stamen as variable, instead of absent, on the basis of Larsen's (1961) report of a wartlike staminode (*stamiodium verruculare*) in *O. siamensis* and *O. laotica* and her own observation of a wartlike staminode in this position in *O. fimbriata*. No trace of a sixth stamen is found at any stage of development in either *O. chinensis* or *O. maxillarioides* (Kirchoff and Kunze 1995). She also revised Kress et al.'s (2001) presence/absence coding of the ovary prolongation by noting that, in addition to the well-developed prolongation that occurs in the Lowiaceae and Strelitziaceae, a prolongation also occurs in the Heliconiaceae, Musaceae, and Costaceae (Kirchoff 1992; Newman and Kirchoff 1992). This makes the possession of a prolongation a primitive character (plesiomorphy) for the order, not a shared derived character (synapomorphy) of the Lowiaceae and Strelitziaceae. The prolongation is, however, much better developed in the Lowiaceae and Strelitziaceae than in the other families, and this extreme development does support the sister group relationship of these two families, as does the lack of a main florescence, discussed above. That they were not placed as sister groups in Johansen's (2005) study is due to the fact that other molecular characters placed the Lowiaceae at the base of the tree, as sister to the rest of the order (Johansen 2005).

Liao et al. (1998) and Wen and Liao (1999) investigated the vascular system of *O. chinensis* and reported that one of the parietal bundles, which normally vascularizes an inner stamen, becomes part of the vasculature of the posterior petal (the labellum). They conclude from this that the labellum is a compound structure, composed of both a petal and a stamen. Our developmental work does not support this conclusion. It is more likely that, as Carlquist (1969) suggests, the path of the vascular bundles is determined by physiological factors and is not a relic of past fusion events. In the case of *O. chinensis*, it seems likely that the lack of a sixth stamen and the enlargement of the labellum have created the conditions under which the labellum has recruited a parietal vascular bundle that would otherwise end blindly.

Acknowledgments

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